

Outbreeding Depression as a Cost of Dispersal in the Harpacticoid Copepod, *Tigriopus californicus*

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Abstract. The costs of dispersing can be evaluated in terms of genetic expenses. These costs are associated with outbreeding depression. In the supralittoral zone of the rocky shore, both outbreeding depression and inbreeding depression may be important in determining whether an organism should disperse. These genetic costs were investigated in the harpacticoid copepod, *Tigriopus californicus*, which inhabits supralittoral pools. Matings between individuals from different pools were performed in the lab. The results suggest high costs to dispersing.

Introduction

In dispersing, any organism will most likely experience some costs. Many of these costs, such as loss of energy while moving, production of dispersal mechanisms, or risk of not reaching a suitable habitat, are ecological in nature and have been fairly well examined (*e.g.*, Palmer and Strathmann, 1981; Strathmann *et al.*, 1981; Cohen and Motro, 1989). There are also genetic costs of dispersing that are associated with outbreeding depression. Individuals choosing mates from different populations may have lower fitness than individuals choosing mates from the same population (*e.g.*, Price and Waser, 1979; Shields, 1982; review by Waldman, 1988). Outbreeding depression will be strongest for individuals in populations that normally have limited gene flow and that live in a heterogeneous environment (*i.e.*, dramatically different selective pressures affect different populations).

In some circumstances, the costs of dispersing must be evaluated relative to the costs of not dispersing. In addition to losing the ecological benefits of dispersing (reviewed by Howe and Smallwood, 1982), individuals may experience genetic costs if they fail to disperse. If individuals

within a population are closely related, inbreeding depression may be a cost of not dispersing (*e.g.*, Greenwood *et al.*, 1978; Packer, 1979; Hoogland, 1982; Holekamp and Sherman, 1989; reviewed by Johnson and Gaines, 1990). Inbreeding depression will be most significant in small, isolated populations; populations that were founded by only a few individuals; or populations that have suffered an extreme bottleneck in size.

Here, I examine a habitat in which both inbreeding depression and outbreeding depression may play important roles in determining dispersal. This habitat is that part of the rocky supralittoral zone that holds small pools of water. Because these pools are above the high tide line, introductions by marine organisms are probably rare. Colonizations occur during relatively uncommon events, such as extreme wave splash or exceptionally heavy rains, which may create channels among pools and access to the ocean. The pools are discrete microhabitats differing from one another in many potentially important characters. These differences are caused often by only small changes in pool shape, tidal height, orientation, or other factors and may generate considerable heterogeneity in selective pressures, such as temperature or salinity, among pools. For example, for 22 pools surveyed on the Oregon coast over 4 months, mean salinity varied from 0.8 to 17 ppt with a range from 0 to 45 ppt and mean temperature varied from 12 to 17°C with a range from 8 to 30°C.

The harpacticoid copepod *Tigriopus californicus* (hereafter called *Tigriopus*) is a common inhabitant of supralittoral pools of the eastern Pacific coast. This organism is ideal for testing hypotheses regarding outbreeding depression and inbreeding depression. There appears to be limited migration of *Tigriopus* among pools. Migration has been documented in streams of water (Cooper, unpub.), which are rare in the supralittoral zone except during storms. Migration has also been observed on the

legs of the shore crab *Pachygrapsus* sp. (Egloff, 1966), which are presumably uncommon on bare rock away from crevices (pers. obs). Limited migration, coupled with abiotic and biotic differences among pools, should promote adaptive differences among *Tigriopus* populations in different pools. Therefore, matings between individuals from different pools (hereafter called non-poolmates) may result in outbreeding depression. Because migrations are probably rare, any pool may be colonized by only a few gravid females, causing many close relatives to be in each pool. The consequences of this founder effect are intensified because of the copepod's breeding system. A female *Tigriopus* will mate only once and can potentially produce 12–14 broods, each with up to 150 eggs (Vittor, 1971; pers. obs.). Therefore, matings between individuals from the same pool (poolmates) may result in inbreeding depression. I investigated the genetic costs to *Tigriopus* of dispersing versus staying in one pool by assaying for outbreeding depression and inbreeding depression in laboratory populations.

Methods and Results

I collected *Tigriopus* 5 km north of Newport, Oregon, from a basalt outcrop near Yaquina Head. I chose six pools from which to collect populations for laboratory mating studies. In choosing pools, I tried to span the range of physical variation to maximize the potential for genetic differentiation among pools, if it exists. Therefore, the pools chosen were different from one another in a maximum number of physical and biotic parameters and should have rarely, if ever, had water flow among them. The pools spanned a horizontal range of >70 m and two distinct outcrops, separated by a rock gully. The characters by which pools differed were salinity, temperature, pool substratum, and pool size (Table I and Brown, 1985). In the lab, I isolated gravid females and their juveniles (as released) from each of the six populations to set up family lines and to assure virginity of the test individuals. The isolated copepods were maintained in 2 ml clear plastic

culture chambers in an incubator at 20°C and at a 16:8 light:dark schedule. They were fed a mixture of Tetramin® flaked fish food and nutritional yeast.

I performed three types of crosses to estimate outbreeding depression and inbreeding depression. The crosses were female × non-poolmate, female × poolmate, and female × sibling. Poolmate matings represent the normal breeding situation for non-dispersing *Tigriopus*. Non-poolmate matings should represent the breeding situation for dispersing copepods; any reduction in fitness in the non-poolmate matings reflects outbreeding depression. Similarly, sibling matings should represent the worst-case result of not dispersing; any reduction in fitness in sibling matings reflects inbreeding depression. However, if pools are full of close relatives, and therefore close inbreeding represents the normal breeding situation, then sibling matings and poolmate matings should have similar results. Furthermore, inbreeding depression is expected to be minimized in this case because many of the deleterious alleles will have been eliminated from the pool population.

After mating occurred in the lab test pairs, I removed the males and placed each female in a large (50 ml) vial with excess food to minimize cannibalism following hatching of the juveniles. From the single mating, females then produced continuous broods. At the end of three weeks (approximately one generation), I counted the total number of individuals (nauplii, copepodites, and adults) in each vial and used this number as a measure of fitness. The rationale for using this number as an index of fitness is that *Tigriopus* probably maximize their fitness most effectively by producing the greatest possible number of offspring. The high fecundity of *Tigriopus* may support this hypothesis.

The number of offspring produced varies with type of cross (Fig. 1). Females mated with random poolmates produced significantly more offspring than did either females mated with non-poolmates or females mated with siblings ($\bar{E}_3^2 = 0.061$, $P = 0.02$). Number of offspring was compared by isotonic regression (see Gaines and Rice,

Table I

Characteristics of pools from which lab populations were taken

Pool	Salinity (ppt) mean (range)	Temperature (°C) mean (range)	Pool size (cm)	Substratum type
1	5.7 (0–15)	14.9 (9–25)	100 × 100 × 17	upright algae, sand
2	9.2 (0–20)	15.9 (9–24)	63 × 28 × 3	algal mat
3	10.0 (0–20)	13.9 (9–20)	45 × 25 × 3	rock, sand
4	17.1 (0–40)	15.6 (9–28)	100 × 50 × 4	algal mat
5	10.0 (0–20)	14.8 (8–27)	100 × 53 × 8	sand
6	9.2 (5–15)	15.2 (9–23)	100 × 100 × 28	upright algae, sand

Mean salinity and mean temperature over a four month sampling period are shown. Approximate pool size is given for maximum values of three dimensions: length × width × depth.

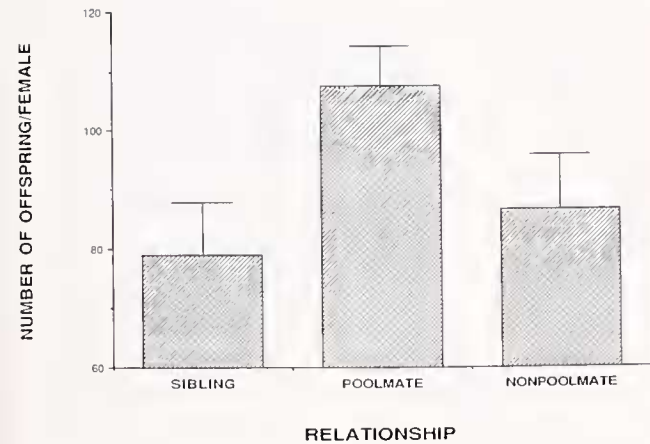


Figure 1. Effect of mate relationship on the number of offspring produced. Columns show the mean number of offspring produced in three weeks by females mated with siblings, poolmates, and non-poolmates. Sample sizes are 30, 37, and 35 females, respectively. Bars represent one standard error.

1990) because the direction of change was specified *a priori*.

Discussion

The results suggest that there are high costs to dispersal in *Tigriopus* associated with outbreeding depression. This result reflects the heterogeneous habitat in which *Tigriopus* live and supports the assumption of limited movement among pools. However, these results are somewhat different from the results of previous studies of *Tigriopus* (Burton and Feldman, 1981; Burton and Swisher, 1984), which demonstrated limited movement among rocky outcrops but high dispersal within any outcrop. The pools I studied are probably most similar to Burton's pools on different outcrops in that there was little or no potential for migration among the pools. Burton (1986, 1990) did find similar costs to outbreeding as evidenced by a decrease in F_2 survival and an increase in developmental time with crosses between populations. The costs of dispersal shown in my study are so great, indeed, that outbreeding depression, due to mating with a non-poolmate, is not significantly different from inbreeding depression due to mating with a sibling.

The results also suggest that a primary benefit of not dispersing is remaining in the proximity of poolmates, which are apparently better mates than non-poolmates. Traditional theory implies that in not dispersing, an individual may suffer inbreeding depression. However, inbreeding depression is not an important cost in the pools because matings between random poolmates result in significantly more offspring than matings between siblings. As previously discussed, if inbreeding were common in pools, then poolmate matings and sibling matings would

result in similar numbers of offspring produced. The results suggest that the gene pool size in each pool population is fairly large.

Mate choice studies in the lab further support the hypothesis that inbreeding in pools is not an important selective pressure for *Tigriopus*. If inbreeding were a strong selective pressure, then identification and avoidance of close relatives as mates might be expected. However, when I presented virgin female *Tigriopus* with pairwise choices of males (sibling + poolmate, sibling + non-poolmate, or poolmate + non-poolmate), they never chose mates significantly different from random (Table II). Nonrandom mate choice probably hasn't evolved because there is no selective advantage to choosing mates in a pool nonrandomly. Pool populations appear to be large enough that siblings are rare as potential mates. A random mate chosen in the pool will most likely be a non-sib poolmate. Nonrandom mate choice or increased frequency of dispersal might evolve when inbreeding depression becomes significant.

In conclusion, dispersal in *Tigriopus* may be costly from a genetic perspective due to significant outbreeding depression. Lack of dispersal (staying in the native pool) does not seem to impose serious genetic costs. These re-

Table II

Results of mate choice tests

Female Choice				χ^2	χ^2
				Relation effect	Stain effect
1. Sibling and Poolmate					
	S	P	Σ		
stained	13	13	26	0.40	3.60
unstained	9	5	14	$P > .50$	$P > .05$
Σ	22	18	40		
2. Sibling and Non-poolmate					
	S	P	Σ		
stained	15	18	33	0.02	1.41
unstained	13	11	24	$P > .90$	$P > .05$
Σ	28	29	57		
3. Poolmate and Non-poolmate					
	P	N	Σ		
stained	12	11	23	0.40	1.40
unstained	10	7	17	$P > .50$	$P > .05$
Σ	22	18	40		

In each test, the female was given a choice of two males—sibling + poolmate, sibling + non-poolmate, or poolmate + non-poolmate. Sample sizes were 40, 57, and 40, respectively. "Stained" males were dyed red with carmine powder to facilitate individual recognition for testing. S = sibling, P = poolmate, and N = non-poolmate.

sults suggest that frequent dispersal may not always be the most adaptive reproductive strategy.

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